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THE INFLUENCE OF TEMPERATURE ON THE SURVIVAL, GROWTH AND RESPIRATION OF CALANUS FINMARCHICUS

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Experiments which have been in progress at the Woods Hole Oceanographic Institution on the nutrition of the ecologically important copepod, *Calanus finmarchicus,* in relation to the food cycle of the sea have shed light on the types of food suitable for this species and on the rate of feeding of which it is capable under different conditions (Clarke and Gellis, 1935; Fuller and Clarke, 1936; and Fuller, 1937). Since the temperatures to which *Calanus* is subjected off our coasts vary greatly with the season and with the locality, it was desired to extend the investigation of the survival and growth of this species in the laboratory to include a larger range of temperature than had been possible previously. In the earlier experiments survival of the copepods had generally been poor, and Gross (1937) has expressed the opinion that even short intervals of temperature change, such as are entailed by the removal of the culture dishes from the constant temperature bath for inspection, are seriously detrimental to animals in culture. In the experiments about to be described we therefore proposed not only to test the effect of a variety of temperatures on growth but also to compare the survival of animals kept continuously at constant temperatures with that of other individuals subjected to periodic changes in temperature.

Calanus was shown to exist in the waters off Woods Hole throughout the year 1935–36 and to undergo reproduction during the spring months (Clarke and Zinn, 1937). Yet food organisms were not sufficiently abundant in these waters to meet the nutritive requirements which we have assumed for *Calanus* even at the maximum rate of feeding observed in the laboratory, if diatoms alone are considered (Fuller and Clarke, 1936; and Fuller, 1937). Food in the form of diatoms appeared to exist in only one-tenth the necessary concentration. This discrepancy has led to such suggestions as the considerable use of the nannoplankton by the copepods and this possibility should be investigated further, but the difficulty could be removed equally well if the

[1] Contribution No. 214.

value assumed for the food requirements of *Calanus* were shown to be ten times too high. The value used was that given by Marshall, Nicholls and Orr (1935) and was calculated from the amount of oxygen taken up by a given number of copepods in unit time. The confirmation of this work was therefore of the greatest importance and we proposed in the present undertaking to repeat the measurements of these investigators, using their own method, and to check them by employing a more precise method. Furthermore, we desired to ascertain whether differences in temperature exert any significant effect on the oxygen requirement of *Calanus* and its application to the nutrition of this species.

Survival and Growth

Material and Methods

For the first group of experiments, which was conducted at Woods Hole during the summer of 1937, copepods were obtained from off-shore localities in the vicinity of Cape Cod. In the second group of experiments, which was undertaken at the Harvard Biological Laboratories in Cambridge, material was obtained off Gloucester. In all cases the copepods were collected by towing a scrim net for a few minutes, and were placed in jars which were kept cold during the trip to the laboratory. Immediately upon arrival the animals were transferred by means of a pipette to covered culture dishes and these were set in baths whose temperature was maintained constant to within 0.5° C. In all the experiments except those involving a change of temperatures (see below) the copepods were transferred each day by pipette to freshly prepared culture dishes (each containing 250 cc. of water) which had been brought to the proper temperature.

The sea water used in the Woods Hole experiments was taken freshly from the harbor (except for the experiments of Table II); that used in Cambridge had been collected at Nahant several months previously and allowed to stand in carboys. In both instances the water was Berkefeld filtered (except for a few tests at Woods Hole in which unfiltered harbor water was used) and then thoroughly aerated.

In most of the experiments a known concentration of food was provided by adding a measured amount of a "persistent" culture of either the diatom, *Nitzschia closterium* (Plymouth strain) or the green flagellate, *Platymonas subcordiformis*[2] to each culture dish. The amount of organic matter represented by these forms and also by the diatom, *Rhizosolenia* sp., which was abundant in Woods Hole waters during the

[2] Kindly identified for us by Professor G. W. Prescott of Albion College, Michigan.

summer, may be judged from the following determinations of nitrogen kindly carried out for us by Dr. T. von Brand:

Nitzschia	2.5 γN	per	10^6	cells[3]
Platymonas	12.7	"	"	"	"
Rhizosolenia	96.0	"	"	"	"

To ascertain whether the number of animals present or the concentration of food organisms was sufficient to affect significantly the dissolved oxygen or the pH of the culture medium, tests were carried out on a representative series of culture dishes as indicated in Table I. The

TABLE I

Tests of pH and O_2 in culture dishes with different numbers of copepods and of food organisms.

Concentration of Nitzschia cells/cc.	Number of Stage V Calanus	pH		O_2 cc./liter	
		Initial	After 24 hrs.	Initial	After 24 hrs.
0	0	8.09	7.86	4.25	5.67
0	10	8.09	7.81	4.25	6.42
30,000	0	8.11	9.09*	4.68	5.94
30,000	10	8.11	7.73	4.68	6.65
300,000	0	8.17	8.10	4.81	6.49
300,000	10	8.17	8.00	4.81	6.37

* This value shown by other tests to be atypical.

results show that sufficient O_2 was present in all containers and that the pH was only slightly altered. The slight increase in O_2 content and decrease in pH in the control was due to incomplete temperature equilibrium initially.

Experiments

The first set of experiments was designed to ascertain whether the *change* in temperature which results from the removal of the culture dishes from the constant temperature bath for daily inspection and transfer of animals has a deleterious effect on the copepods. For this purpose groups of *Calanus* and also of *Centropages typicus*—another copepod common in the Woods Hole region—were divided into two parts and placed in culture dishes in constant temperature baths maintained at either 8° C. or 13° C. One culture dish in each group was left undisturbed in the bath as a control but others were removed for varying lengths of time as indicated in Table II. For the duration of

[3] The reason why this value is larger than that found the year before and reported by Fuller (1937) is not known. Variations of this sort must be taken into consideration in calculating the potential food value of each species.

the experiments the survival of *Calanus* was better than that of *Centropages* but in neither case was survival in the control dishes significantly better than that in the dishes which were subjected to a daily temperature change. We conclude, therefore, that contrary to the suggestion of Gross (1937), the daily inspection at room temperature is not harmful in our experiments with these copepods.

Our next set of experiments was designed to test the effect of the concentration of food organisms on the survival and growth of *Calanus* at temperatures of 7° or 8° C. For this purpose culture media were prepared in which the concentration of food organisms differed by

TABLE II

Effect of *change* of temperature on survival. Comparison of number of deaths in cultures removed from constant temperature bath for daily periods of varying lengths with number of deaths in cultures not removed. Two hundred and fifty cc. Berkefeld filtered sea water from tap in each culture dish, left unchanged, and no food added. Experiments carried out in July, 1937 at Woods Hole.

Species	Initial no. of animals in each culture dish	Temp. of constant temperature bath	Period culture removed from bath each day	Temp. of culture when replaced	Duration of experiment	No. of deaths
		° C.		° C.	days	
Calanus (Adults)*	10	8.5	30 minutes	14.0	8	1
" "	10	8.3	not removed		8	3
Calanus (Stage V)†	15	8.0	60 minutes	16–19	7	0
" "	15	8.0	not removed		7	1
Centropages (Adults)*	20	8.5	30 minutes	12–15	8	17
" "	22	8.5	120 "	16–21	8	15
" "	20	8.2	not removed		8	12
" "	20	13.3	30 minutes	15–18	8	18
" "	20	13.3	120 "	20–21	8	20
" "	20	13.0	not removed		8	18

* Animals obtained at Whistle Buoy at western entrance to Vineyard Sound.
† Animals obtained at South Channel, east of Nantucket.

very large amounts (Table III). Ten to twenty-five *Calanus* were introduced into each culture dish and their condition noted each day for the duration of the experiments (2 to 4 weeks). The daily transfer of animals to freshly prepared culture media prevented an appreciable change in the concentration of the food from being brought about by either the grazing of the animals or the multiplication of the food organisms. Accumulation of metabolites was similarly avoided.

In this set of experiments no copepods were observed to moult successfully but certain individuals reached the moulting stage and died during the casting of the shell. As in previous investigations, the number of animals which began the moulting process may be taken as an index of growth. The reliability of this procedure is strengthened by the fact that low numbers of "deaths in moult" are usually accompanied by high numbers of "deaths not in moult" and vice versa (see Table III). On this basis our results reveal the best nutritional conditions in those cases where 30,000 cells/cc. of *Nitzschia,* or more, were provided, but a concentration as high as a million and a half cells/cc. appeared harmful. The moulting stage was attained (i.e. "deaths in

Table III

Effect of concentration of food on survival of *Calanus.* Temperature of constant temperature bath for experiments in July and August: 8° C., in September: 7° C. Each group of animals placed in 250 cc. of culture medium. Animals in copepodid Stage V. Experiments conducted at Woods Hole in 1937.*

Food organism	Conc. of food	Exper. begun	Exper. concluded	Initial no. of copepods	Deaths in moult	Deaths not in moult
	cells/cc.					
Nitzschia	300,000	July 11	Aug. 9	15†	8	5
"	150,000	"	"	15	10	4
"	30,000	"	"	15	8	3
"	15,000	"	"	15	4	8
none		"	"	15	4	8
Nitzschia	1,500,000	Aug. 15	Aug. 31	25‡	0	25
"	150,000	"	Sept. 3	25	1	13
"	1,500	"	"	25	4	16
none		"	"	25	0	11
Unfiltered	harbor water	"	"	25	0	22
Platymonas	18,000	Sept. 11	Sept. 31	10‡	0	7
"	4,500	"	"	10	0	6
Nitzschia	230,000	"	"	10	0	9
none		"	"	10	0	6

* Experiment begun September 11 carried out with the assistance of Mr. Dean F. Bumpus, biological technician for the Woods Hole Oceanographic Institution.

† Animals obtained from South Channel, east of Nantucket.

‡ Animals obtained from Cape Cod Bay, 4 miles NNE of Canal.

moult") in a higher proportion of cases in the tests begun on July 11 than in those begun on August 15 and in the experiment of September 11 not a single copepod reached the moulting condition. Indication that the animals stopped feeding toward the end of the season arises from the fact that no significant difference was observed in the survival in different food concentrations for the September 11 experiment. Moreover, in this case and in the experiment of August 15 the unfed controls fared as well or better than the copepods which were provided with food. This suggests that the feeding or the survival (or both) of the copepods may depend upon the season because of differences in the phase of the life cycle characterising the copepods at the time the experiments were begun (see below).

With the possibility of a seasonal effect in mind, arrangements were made for the next set of experiments to be conducted during the spring months when *Calanus* off our shores is known to be breeding and growing (Fish, 1936; Clarke and Zinn, 1937). In nine tests at three temperatures and with varying amounts of food using copepodid stage IV and in three tests using copepodid stage III, run in exactly the same manner as the experiments of the previous summer, survival was good and a considerable amount of moulting took place (Table IV). In the case of stage IV the number of successful moults at 3° C. did not differ materially with the amount of food provided, but at the other

TABLE IV

The effect of temperature and food concentration on the survival and growth of *Calanus*. Animals obtained off Gloucester. Each group placed in 250 cc. of culture medium. Experiments conducted at Harvard Biological Laboratories in 1938 with the assistance of Mr. Dean F. Bumpus.

Jar	Temp.	Conc. of Nitzschia	Initial population April 22. Copepodid stage	Successful moults	Deaths in moult	Deaths not in moult	Final population May 18. Copepodid stage
		cells/cc.					
1	3° C.	150,000	10 IV	5	0	1	1 IV, 7 V†
2		1,500	8 IV, 2 III	4	0	2	2 IV, 6 V
3		0	9 IV, 1 III	5	0	3	2 IV, 4 V†
4	6° C.	150,000	11 IV	10	0	5	3 V, 3 VI♂
5		1,500	10 IV	6	0	5	3 V, 1 VI♂, 1 VI♀
6		0	8 IV, 2 III	0	1	9	0
7	9° C.	150,000	9 IV, 1 III	7	1	4	1 V, 1 VI♂, 2 VI♀†
8		1,500	10 IV	5	1	5	3 V, 1 VI♀
9		0	10 IV	2	1	8	1 V
10*	3° C. then 9° C.	1,500	10 III	4	1	6	2 V†
11	6° C.	1,500	10 III	2	2	7	1 V
12	9° C.	1,500	10 III	6	0	1	?‡

* At the end of 7 days at 3° C. no animals had moulted and none had died. The jar was then transferred to 9° C.

† One animal missing.

‡ Animals accidentally lost on the seventh day.

temperatures a distinct positive relation was found between the growth of the animals and the concentration of *Nitzschia*. The largest number of animals moulting occurred in the culture with high food concentration at 6° C. (Jar 4). Deaths during moult took place chiefly at the high temperatures. Deaths not in moult were much more abundant in the cultures not provided with food and were confined largely to the higher temperatures.

Of the stage III animals, all of which were provided with the same amount of food, the group at 9° C. was accidentally lost on the seventh day but six in this group had already moulted. In contrast, there were no signs of growth by the seventh day in the group at 3° C. However, after the latter animals had been transferred to the 9° bath, four moults occurred within six days. In the culture at 6° C. there were two successful moults and two deaths in moult. Three of the stage III animals attained stage V, thus having passed through two moults. In the case of the copepods which were in stage IV at the beginning of the experiment, nine individuals (in the 6° and 9° cultures) moulted twice and thus reached the adult condition (stage VI).[4] From the results of this set of experiments we may conclude that at 3° C. moulting was retarded but at the same time survival was good. A larger number of successful moults and deaths in moult occurred at 6° C. and about the same proportion at 9° C. but at these temperatures survival was definitely inferior to that at 3° C.

Respiration

Material and Methods

The copepods used for the experiments on respiration were taken by tow net in Cape Cod Bay and placed in large jars packed in ice for the return run to the laboratory. Vigorous specimens of copepodid stage V were then picked out by pipette, transferred to culture dishes and placed in the refrigerator at 8° C. until the tests were begun on the following day. The sea water used for the cultures and for the experiments was taken in carboys at the point where the animals were collected (except for the tests at 16.8° C. in which the laboratory salt water supply was used). In all cases the sea water was Berkefeld filtered and aerated before use. No food was added.

Respiration was measured by the Winkler method and in other tests by a manometric method in which a respirometer of the Dixon-Haldane constant pressure type was used. In the former case almost exactly the same procedure was followed as that described by Marshall, Nicholls, and Orr (1935) except that in the tests reported below 25 and

[4] Under the microscope the gonads of both sexes were observed to be ripening at the end of the experiment.

75 animals were used respectively in 200 cc. of water instead of the 120 animals employed by the earlier workers. In the latter case the apparatus was arranged as outlined by Dixon (1934) with the exception that no KOH well for the absorption of CO_2 was used. Tests showed that no difference in the changes of value of the gas within the apparatus occurred when the KOH well was removed. It is probable that over the short periods of time involved the small amount of CO_2 produced was readily absorbed by the slightly alkaline sea water. In our apparatus all joints were of ground glass and were carefully sealed with stopcock

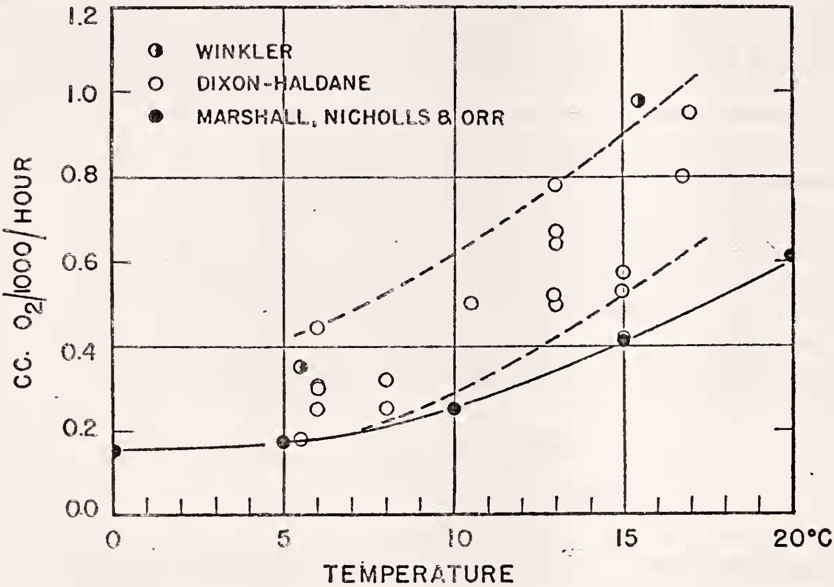

Fig. 1. Relation between temperature and amount of oxygen consumed by stage V *Calanus*. Dashed lines give the limits of all determinations with the Dixon-Haldane respirometer. Experiments carried out at Woods Hole during August and September, 1938.

grease or vaseline. The respiration flasks were completely immersed in a constant temperature bath controlled to 0.5° C.

In the experiments which follow 6 to 30 animals were placed in 10 to 20 cc. of water in one of the respiration flasks. This flask had been painted black to exclude light since Marshall, Nicholls, and Orr reported that differences in illumination exerted a marked influence on the rate of respiration. Equilibrium between the liquid and the gas above it was attained by attaching the entire apparatus to a Warburg shaker. Since continuous or rapid shaking resulted in poor survival of the copepods and might influence abnormally the rate of respiration, the shaking was limited to the 5 or 10 minutes immediately before each reading and was confined to an amplitude of 2 cm. at a frequency of 100/min. Readings were ordinarily made every 20 minutes for 4 or more hours. The change in volume for each period was observed and reduced to cc. dry gas at N. T. P. Blank trials, which were run at intervals in exactly the same way but with no animals, showed no variation in volume over periods as long as 4 hours. In certain cases water in which copepods had been living and which presumably contained

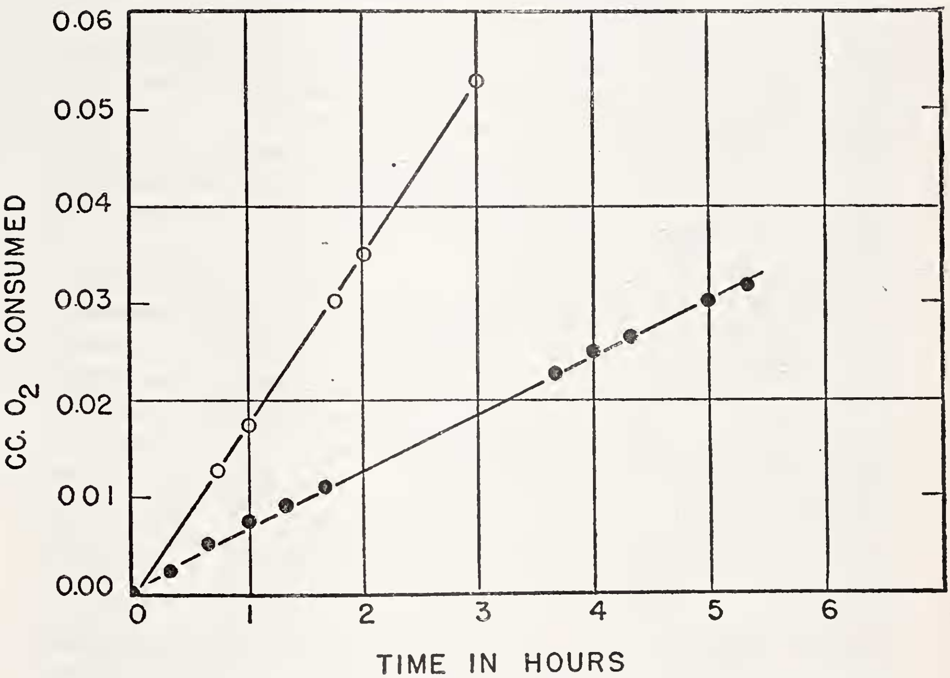

Fig. 2. Progress of two typical experiments on consumption of oxygen by stage V *Calanus*. Closed circles: 6 animals at 16.8° C. Open circles: 28 animals at 13.0° C.

a characteristic number of bacteria was used for the blank tests. Thus assurance was provided that in the experiments neither microörganisms nor other extraneous agents were interfering appreciably with the results.

Experiments

Two measurements of the oxygen consumption of *Calanus* were made using the Winkler method. The first of these was carried out at 5.5° C. using 25 animals confined in 200 cc. of sea water for 4 hours and yielded a value of 0.35 cc. O_2/hr./1,000 copepods. In the second case 75 animals in 200 cc. were tested at 15.5° C. for 4 hours and were found to have consumed oxygen at the rate of 0.98 cc. O_2/hr./1,000 copepods. The first of the values is somewhat higher and the second is considerably higher than those obtained by Marshall, Nicholls, and Orr (1935), as may be seen in Fig. 1.

The experiments using the Dixon-Haldane respirometer comprised 17 tests carried out at 7 temperatures ranging from 2.5° C. to 16.8° C. In each test from 4 to 12 readings were made during the course of the run and these were plotted against time, as in the two typical experiments shown in Fig. 2. The fact that these curves and all the others which have been used in the calculations exhibited only a slight deviation from a straight line shows that the consumption of oxygen was sensibly constant over the period of each experiment. Marshall, Nicholls, and Orr reported a drop in oxygen consumption during the first 10 or 15 hours after the capture of the copepods but in our experiments, since measurements were not begun until the day following capture, this period of decreasing respiration was avoided.

From the average slope of each curve of oxygen consumption a value was obtained which was converted into cc. O_2/hr./1,000 copepods and the results plotted in Fig. 1. It will be observed that a considerable variation exists among the several tests at the same temperatures. Evidently respiration in *Calanus* can vary between wide limits and this conclusion is borne out by the observations of the earlier investigators. However, there is no doubt as to the general magnitude of the oxygen requirement of *Calanus* in the present experiments. The influence of temperature on respiration is indicated by the upward slope of the dashed lines in Fig. 1 enclosing all the points. The values increased from an average of about 0.32 cc. O_2/hr./1,000 copepods at 5.5° C. to about 0.91 cc. O_2/hr./1,000 copepods at 16.8° C. Although our measurements give a somewhat higher average rate of respiration at all temperatures than was obtained by Marshall, Nicholls, and Orr, they are of the same order of magnitude. Furthermore, there is no indication of a possible lower oxygen requirement for the Woods Hole copepods since *every one* of the present values was higher than those obtained by the British investigators.

Discussion

The foregoing experiments not only have confirmed and illuminated the early work at Woods Hole, but in addition have raised a number of new questions. It is clear that both the amount of food and the temperature have an important influence on the growth of *Calanus* and on its survival.[5] The situation is further complicated by the fact that under conditions which tend to promote growth, survival may be poor because of the likelihood of death during the moulting process. The provision of food improves growth and survival, but the exact amount of food seems not as important as originally supposed (cf. Clarke, 1939). Although a minimum was ordinarily required for growth, in certain experiments at low temperatures some moulting was observed in the entire absence of food. And in at least one case a very high concentration of food was found to be harmful (see also Lucas, 1936).

It is a striking fact that a large amount of moulting took place and good survival was observed in our experiments conducted in April and May (Table IV) whereas poor survival and no successful moulting was the rule for the tests made during the summer and early autumn (Table III) and for the summer experiments of Fuller (1937, Table V, temperature 13° C.).[6] In all cases *Nitzschia* was used as the food organism in at least some of the cultures, the temperatures of the cultures were not widely different, and exactly the same procedure was followed. For the April and May tests copepods were obtained from a point off Gloucester but in two of the other cases the experimental animals were procured from a location which was also north of Cape Cod although considerably to the south of Gloucester.[7] If the place of origin of the copepods is immaterial, it might be suggested that the time of year at which the animals were collected could have an important bearing on the laboratory results. According to the observations of Clarke and Zinn (1937) and of Fish (1936) the second of the two yearly broods of *Calanus* grows to copepodid stage V during the summer and remains in that stage until the following January or February. It seems possible that in nature feeding may be reduced to a minimum and mortality may be especially high during the late summer and that animals collected during this period might exhibit poor survival and refuse to grow even under the most favorable laboratory conditions. Added support for this view is derived from the fact that in our experiment begun September 11 (Table III) no successful moults occurred and no animals were observed even to attempt to moult.

[5] In fact Fish (1937) is of the opinion that the presence of suitable temperatures is the most important factor in the production of zoöplankton in the Gulf of Maine and the Bay of Fundy.

[6] In the earlier summer experiments of Clarke and Gellis (1935) and of Fuller and Clarke (1936) growth and survival were better, but the different methods used make comparisons inappropriate.

[7] The following ocean temperatures were observed:

Off Gloucester, April 26, 1938, 9.6° C. at surface.
Cape Cod Bay, August 14, 1937, 18.3° C. at surface, 10.2° C. at 15 m., 8.6° C. at 30 m.
South of Cape Cod temperatures were generally higher.

In all of our experiments at Woods Hole and especially in those described above the copepods were noticed to be heavily parasitized immediately after death. An animal which appeared perfectly healthy one day would be found dead on the next day with its body filled with opaque whitish or colored masses. Possibly parasites gain a foothold within the copepod and remain unnoticed until they suddenly reach some vital tissue. From this initial infection the rapid and obvious spread of the parasite to all parts of the body could be accomplished after death within a relatively short interval. Since Jepps (1937) reported that a large proportion of *Calanus* population was found to be infected when collected, it is possible that the inroads of parasites may be an important element underlying the fluctuation in the abundance of this species both seasonally and annually.

The experiments on respiration show that the values which have been used for the oxygen consumption of *Calanus* and hence its food requirement, are of the correct order of magnitude. In fact, our measurements indicate that an even larger amount of food per day is required by these organisms than was assumed by Marshall, Nicholls, and Orr. Therefore, the discrepancy between the nutrient required and the number of diatoms available for food gapes wider than ever. According to Harvey (1937) *Calanus* can filter out the larger species of diatoms much more effectively than the smaller forms. He found that 100 times the volume of water may be swept free in an hour when *Lauderia* or *Ditylium* were provided as food as when *Nitzschia* was used. However, in nature the larger diatoms are not as abundant as the more minute species, and a careful investigation of the amount of food per cc. of sea water which the scarcer but more bulky types would provide is seriously needed. Another point which needs study is the " micro-distribution " of the phytoplankton and nannoplankton. Although uniformity in abundance may be found in a series of one-liter water samples taken from an area, the distribution *within* each liter may be highly irregular. If the food organisms occur in clusters, and if a copepod can find and stay in a local though minute zone of abundance, sufficient nutriment could be obtained without the necessity of filtering an excessive volume of water. Such explanations as the foregoing may resolve the discrepancy between the daily food requirement and the *average* abundance of potential food organisms.

Summary

Laboratory tests on cultures of *Calanus* in relation to the ecology of this species showed that: (a) removal of the culture dishes from constant low temperature to room temperature for daily periods as great

as 120 minutes was not harmful to the copepods; (b) growth was poorer at 3° C. than at 6 to 9° C. but survival is better at the lower temperatures; (c) both growth and survival decreased regularly in passing from experiments conducted in the spring to those in the autumn.

Measurements of the respiration of *Calanus* using the Winkler method and the Dixon-Haldane respirometer showed that the magnitude of the oxygen requirement for our animals is of the same order as for those tested by Marshall, Nicholls, and Orr, and possibly is higher than previously reported. The discrepancy between the estimated food requirement of *Calanus* and the average abundance of diatoms therefore still exists but certain possible explanations are discussed.

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